Additional Peculiarities in the Spermatogenesis of Phrynotettix Magnus

by David Henry Wenrich

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Submitted to the Department of Zoology of the University of Kansas in partial fulfillment of the requirements for the Degree of Master of Arts

SPERMATOGENESIS OF PHRYNOTETTIX MAGNUS

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(Outline)

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ADDITIONAL PECULIARITIES IN THE SPERMATOGENESIS OF PHRYNOTETTIX MAGNUS.

I. Introduction.

a. Purpose and scope.

In 1908 there was published a paper by Miss Edith Pinney (8), based on observations made in this laboratory, describing the peculiar polar granules found to exist at the synaptic ends of the chromosomes in the male germ cells of Phrynotettix magnus. On further examination this species was found to possess other interesting peculiarities and was also found to present possibilities for determining the details of the process of synapsis. (By synapsis I mean the union of spermatogonial chromosomes in pairs to form the reduced number found in the spermatocytes.) Further study of the spermatogenesis of Phrynotettix was undertaken therefore with a two-fold purpose in view: First, to become acquainted with the additional peculiarities of the species and thus add to our knowledge of the spermatogenesis of the members of the family Acridadae for comparative purposes; and Second, to follow, if possible, the details of the process of synapsis.

It is with the first of these purposes that the present paper will deal primarily. It is by no means presented as an exhaustive study of this form, however. Indeed, several inter-

esting details are now under consideration which have not yet been worked out sufficiently to warrant description at the present time and they must be left for the future. With the second of the purposes mentioned above, the writer hopes to deal in a subsequent paper.

b. Materials.

The material used consisted partly of the slides prepared by Miss Pinney and partly of additional slides prepared by the writer from testes furnished by Dr. McClung. All of the material was collected in 1907 in Arizona, fixed in Flemming's stronger fluid and preserved in 70% alcohol. Heidenhain's Iron-Haematoxylin and Flemming's tricolor stains were both used to good advantage. In all, the testes of about eight individuals were available for study. For comparative studies I had access to Dr. McClung's collections of slides.

c. Acknowledgements.

Before going further I wish to acknowledge gratefully the encouragement and helpful suggestions given by Dr. McClung, under whose direction the work has been done, and to express my appreciation of some colaboration by Miss Eleanor Carothers, who first noticed and called to my attention the occurrence in several other species of some of the peculiarities here described for Phrynotettix.

II. The Polar Granules and Continuous Spireme.

A. Polar and Composite Granules in Phrynotettix.

a. Review of Miss Pinney's paper.

One of the most striking peculiarities of Phrynotettix magnus is the occurrence of large granules at the polar ends of the chromosomes in the different generations of the male germ cells. In order to have before us a complete description of these interesting bodies it seems desirable to present here a summary of Miss Pinney's paper.

In the spermatogonial divisions she found that in the early telophase the accessory precedes the other chromosomes in the formation of vesicles and the diffusion of the chromatin and it is therefore the first to show a polar granule. She says: "The diffusion of chromatin within the accessory (vesicle) discloses to observation a small black spherical granule lying close to the vescicular membrane at the proximal end. This granule is always seen in the accessory in this stage and always at the polar end." (As in Fig. 5) Similar deeply staining granules were found in the other chromosomes and, "it is noteworthy that these bodies occur only at the polar ends." In the early growth period she finds that "The accessory chromosome, a shapeless mass of homogeneous chromatin, lies at one side of the cell. Near it and next to the nuclear wall is a group of bodies re-

sembling the accessory in all but size, being much smaller. From these the chromatic threads extend outward, each segment apparently forming a loop the ends of which have their termination in the small chromatin bodies." The description of these bodies is next taken up in connection with the early tetrads, which have just been formed from the spireme loops. She says, "The interesting and peculiar feature of these formations are the condensed bulbous thickenings marking the synaptic end of each chromatid. - - - Oftentimes these peculiar enlargements occur at each end of the chromatids. This is confusing and in the light of my limited observations is unaccountable." After the first spermatocyte division, the telophase shows "in the ordinary dyads - - - - - granules in their synaptic ends staining similarly to those previously noted in the spermatogonial divisions." In the spermatid in the stages closely following the second spermatocyte division she found "persistent bodies of chromatin distributed irregularly through the less concentrated nuclear substance." The continuity of these polar granules through many of the various stages was thus established by Miss Pinney, and in her conclusion she says, "We may, I think, safely conclude that every chromosome is definitely and unchangeably polarized and that the point of the spindle fiber attachment is constant. - - - - I am convinced that in the small bodies of

condensed chromatin in the early spermatocyte prophases we have the direct product of two conjugating polar granules. - - From these observations it appears that the polar granules are permanent bodies, not undergoing marked physical change during the process of cell division. This permanency of position in the case of the polar granule seems to indicate the existence of a fate which governs the relative position of the constituent elements of the chromosome through its various changes. - - - Unquestionably they (the granules) are in some way concerned with the definite polarization of the complex element to which they belong, and their relations both to the spindle fiber and to synapsis is significant."

The observations of Miss Pinney here recorded were confirmed by my own studies in nearly every particular. What I have to say regarding these polar granules will be a few additions to the series of facts just set forth.

b. Composite Granules in the Growth Period.

I find that in the stages immediately following the beginning of the growth period, following the last spermatozonial division (leptotene stage), there is a tendency for the polar granules to fuse together to form a composite granule. This stage is shown by Miss Pinney's figs. 16 + 17 and my figs. 16, 19. This joining of the polar granules forms usually, as seen in the later stages, a large mass of condensed chromatin with the spireme fibers radiating out from it. To this mass the accessory

is usually attached, sometimes by a slender prolongation of its chromatin substance, sometimes by a thicker connection, and sometimes the union is so intimate as to result in partial or entire fusion of the two bodies. These variations are shown by figs. 21 to 26. Similar situations are shown in Miss Pinney's figs. 19 + 20, although she did not recognize the composite granule as such.

Not all of the granules take part in the formation of this large composite granule, however, as the figures will show, and indeed the number that do fuse in this way seems to vary. Some of them may unite to form smaller composites and it also seems that some of them may remain independent, never uniting with any of the others. In the earlier stages, as shown by figs. 16 to 19 the polar granules are all on one side of the nucleus, indicating a definite polarity of the nuclear substance. As the growth period advances, however, those granules which are not united to the large composite granule in many cases tend to drift away from its vicinity, so that granules may be found in various parts of the nucleus. Usually not more than eight radiating threads can be counted as proceeding from the largest composite granule, and the number shown by others is usually two, four, or six.

The accessory does not always remain attached to the large granule and it may often be seen at various distances from it and sometimes on the opposite side of the nucleus. Usually an indefinite number of granules remain attached to the accessory

as is indicated by a small and indefinite number of threads connected with it. It is also certain that the individual granules vary in the relationships thus shown, but this point will be discussed in connection with the precocious spireme loop soon to be described.

c. Composite granules in later stages.

At the end of the growth period the composite granules are seen to break up into their component parts, each with its thread attached. (Fig. 31) Their persistence at the ends of the tetrads formed from the spireme is shown in figs. 32+33 where the situation closely resembles that in Miss Pinney's fig. 18

The reappearance of the granules in the telophases of the two maturation divisions is recorded by Miss Pinney as noted above. There is also some indication of a composite granule in the young spermatid as shown in fig. 36.

The persistence of the polar granules through the stages from ~~final~~ final spermatogonial division to spermatid is thus seen to tally with the results as obtained by Miss Pinney, as quoted above. Their appearance and existence through the spermatogonia was well established by Miss Pinney, and is shown also in figures 8 to 12 of this paper. The union of these granules into composite granules, however, was apparently overlooked by Miss Pinney, although her figures indicate this condition.

d. Composite granules in other kinds and generations of cells.

The appearance of the composite granule is not restricted, however, to the stages following the last spermatogonial division. It may be found in the telophase of all the spermatogonial generations as shown by figure 3 which is of one of the earlier generations, and even in the same phases of the follicular and connective tissue cells (figs. 1 & 2). This tendency of the polar granules to coalesce in the stages where the rest of the chromatin is diffused or strung out in long threads might be interpreted to represent a persistent polarity of the nuclear substance through all generations and stages. It is at least additional evidence of the precise though complex organization of the nucleus.

Figures 8 & 9 show granules at the distal ends of the chromosomes as well as the proximal. Their occurrence in this way may explain the presence of the granules at both ends of the tetrads when the latter are first formed at the end of the spireme stages, (Figs. 32&33), a fact mentioned by Miss Pinney and often observed by myself. It could be assumed that the union at the distal ends of one or two pairs of chromosomes is accompanied by a condensation similar to that at the proximal end.

B. The Continuous Spireme.

a. Continuous spireme in the last spermatongonia.

The existence of a continuous spireme is a matter of considerable importance in view of its bearing on synapsis which is attracting so much attention at the present time. In his early

study on the Acridadae McClung considered the spireme as probably continuous in the growth stage, but could not demonstrate its existence.

Sutton (9, 10) working on Brachystola held that a telosynapsis of paired chromosomes took place but no continuous spireme was formed. Davis (2) more recently working on Acridadae states repeatedly and emphatically that no spireme exists. Its formation in Phrynotettix, however, is so plainly evident that no one seeing the end to end union in the spermatogonial telophases could deny its existence. Indeed I have found it in a species of Dissosteria, a species of which genus Davis made the object of his chief observations.

Figures 5, 6 & 7 show the process of spireme formation as it takes place in the telophase of the last spermatogonia. The noticeable absence of definite polar granules is to be explained by the small degree of diffusion that the chromosomes have undergone at this time.*

Figure 5 strongly indicates that the union of the proximal ends precedes that of the distal ends. Many cells in the same cyst, however, showed the chromosomes united at both ends. Sutton (9,10) found in Brachystola the proximal union but failed to see the distal one. This figure would also indi-

*It should be noted here, however, that the size and prominence of the granules may vary with different methods of fixing and staining and with different individuals.

cate that the pairs of chromosomes are united at their prosimal ends. The appearances in other cells, however, does not permit of a definite conclusion on this point. I find as many instances where the two limbs of a united pair are equal with respect to the distal end as where the converse is true. Furthermore, in contradiction to the evidence furnished by figure 5 the precocious spireme loop described below would suggest the union of pairs at their distal ends. A full discussion of the relation of this question to synapsis will be taken up later.

b. Spireme in other generations of cells.

Not only do the chromosomes unite end to end in the telophase of the last spermatogonia but the same can be seen in the telophases and prophases of all the spermatogonial generations. Figure 4 for example, is of a prophase in an early generation, and similar appearances are seen in the primary spermatogonia surrounding the apical cell.

The fusion of some of the polar granules in these cells has already been mentioned and the direct relation between this and the continuous spireme is, I think, apparent. In the follicular and connective tissue cells, (Fig. 1 + 2) the arrangement of the threads in the telophase, the presence of the composite granule, and the actual union which may be seen at the proximal ends of the chromosomes strongly suggest the presence of a continuous spireme there also.

The question as to whether this end to end union of the

chromosomes is the sum of the synaptic processes or whether, as so strongly maintained by Gregoire (12) and others, another process of parasynapsis takes place, will be postponed for future discussion.

C. Polar Granules in Other Species.

The interesting behavior of these polar granules in Phrynotettix led to a search for them in other species, especially among the Acrididae. They were found to exist in a considerable number of the forms examined although in none of them were they as prominent as in Phrynotettix. A great many of the slides examined did not show stages favorable for the display of the granules, and while the proportionate number that did show them was rather small, I am inclined to think that more favorable preparations would show their presence quite generally throughout the Acrididae.

The granules show most prominently at the beginning of the growth period where their condensed condition is contrasted with the slender and comparatively faintly staining threads. In this stage the granules were found in Brachystola, Arphia, Stenobothrus, Hippiscus, Amphitornus, Mermiria (two species), Eremnus, Tropidolophus, Pseudopomala, and Hesperotettix. In some of these forms a composite granule was found in the growth period as is true of Brachystola, Hippiscus, Eremnus, Amphitornus, Stenobothrus, Pseudopomala, Tropidolophus, and I believe that favorable pre-

parations would show it in the others.

Nothing of the kind was found in the few examples of the Locustidae that I examined but in a slide of Gryllus I found a well formed composite granule, or a body in the growth period at the center of the rosette which I consider homologous to it, (Fig. 40), although it was not mentioned by Baumgartner (1). The history of the formation of this body in Gryllus could not be determined from the slides at my disposal but it may well be inferred that it arose, as in the Acridadae, from a fusion of polar granules.

The Chromoplast of Janssens (3) as figured in his paper on Batrachoseps appears from his description and figures to arise in the same way as does the composite granule just described. I therefore conclude that it is of the same nature. His figures show the enlarged deeply staining nabs on one end of the chromatids after the spireme has broken up.

It should be noted here that the rosette or bouquet condition of the spireme in the growth period has been recorded for a great many different animals, showing that it is of fairly general occurrence. In Phrynotettix and other forms having the polar granules, the composite granule or "chromoplast" is at the center of the rosette. The arrangement is essentially the same in all and indicates a persistent polarity of the nuclear substance so long as the rosette persists. In Phrynotettix it per-

sists until the formation of tetrads from the spireme is begun. It might also be inferred that all those forms showing the rosette or bouquet in the growth period may have a common type of synapsis, since the relation of the threads seems to be the same. The preparations of some of the species of grasshoppers that I have examined show, however, this rosette condition much less definitely than is seen in Phrynotettix and Brachystola.

III. The Precocious Spireme Loop and Tetrad.

A. General Description.

One of the spireme loops of the growth period is very prominent by reason of its greater degree of condensation and consequently strong staining capacity. Its identity is unmistakable throughout the growth period and well into the following prophase. One of the metaphase chromosomes is always precocious in its division and I feel confident that it is the same element. Here (in the metaphase) the longitudinal division of the tetrad has progressed so far that when it reaches the equatorial plate it is in the form of a long rod. This rod may exhibit either a slight enlargement or a slight constriction in the middle, depending upon just how far advanced its division is. Figure 34 shows this element in the metaphase. The figures also show one of the other tetrads advanced to a similar condition though not quite so far. These two elements maintain this relative degree of advancement toward complete division in all the metaphase

cells. A similar precocious metaphase rod appears in the other species that show a similar precocious spireme loop and also in some other species where unfavorable preparations did not show a precocious loop differentiated in the growth period. Miss Nowlin (7) described such a precocious metaphase rod for Melanoplus bivittatus, but a corresponding differentiated spireme loop is not described.

In the telophase of the first spermatocyte, the same element shows quite prominently as a well formed though roughened dyad, as shown in figure 3 5, while all the other chromosomes except the accessory have undergone extensive diffusion. Attention is here called to the similarity of behavior between this element and the accessory dyad. The latter is only a little more condensed and definite in outline than the former. (It will be noticed that I called the stage shown in figure 3 5 a telophase. As to its being a telophase of the first or a prophase of the second division I cannot be absolutely certain. Since, however, I have found no stages of the telophase where the accessory and this precocious element were more diffused than the other dyads, I have assumed that they do not undergo as great diffusion as do the others, hence the reference to this stage as a telophase.)

Again in the young spermatid a mass of chromatin which is more tenacious of its individuality and more condensed and deeply staining than any of the other chromosomes, except the

accessory and polar granules is probably the same individual. The element is possibly indicated also by the second darkly staining mass indicated at "g" in figure 3=/2 in the telophase of the last spermatogonia. Its differentiation at this stage would not be unexpected in view of its following to some extent the behavior of the accessory in some of the other stages.

B. Behavior in the Growth Period.

It is of the behavior of the precocious loop in the growth period that I wish to speak more especially, in view of the possibility of its being typical of all the spireme loops. The statements to follow will assume that the polar granules heretofore described do actually occur at and represent the polar ends of the chromosomes during this growth period as elsewhere; that this precocious loop is a complete one with a granule at each end; that the polar granules of the growth period represent a pair of those that were at first separate and then conjugated in the telophase of the last spermatagonia; that the composite granules represent the combined and fused mass of two or more of these double granules. That these assumptions are justified, I think the evidence presented shows.

It is somewhat surprising to find that not only do the number of granules in a composite vary, but that the individual granules so united are not the same for any composite. In other words, the composites in different cells are not identical. This

is shown by the behavior of the precocious loop. For example it may have both ends attached to the largest composite granule; it may have one end attached to the accessory and the other to one of the composite granules; it may have both ends attached to the accessory, or it may have both ends united together to form a small composite granule to which only two other spireme threads are attached. Just why such a diversity of relationships between the elements of the spireme should obtain, is difficult to understand. That such a diversity does not modify to any great extent the net results is shown by the uniformity presented by the metaphase groups that follow. One is almost forced to conclude that the "personnel", if I may use such a term in this connection, of any united group of granules is governed by chance proximity and that subsequent fusion is accomplished only between those which happen to be favorably placed near each other. Also one, I think, is justified in concluding that the union at the ends of the chromosomes is the important and therefore persistent one while the formation of composite granules is of only secondary importance. This latter conclusion is also supported by the fact that the number of threads radiating from any composite granule, of whatever size, is practically always even, showing that the polar union accomplished in the spermatogonial telophase is persistent.

C. Comparison with Accessory.

I wish to call attention here to the somewhat remarkable parallelism between the behavior of this precocious element and the accessory. But before entering upon this comparison I should say a word about the behavior of the latter element in this species.

The accessory as first described for the Acridadae, it will be remembered, was thought not to enter into the spireme condition at all. Later it was found that a modified spireme condition did exist, thus placing it more closely in the same catagory with the other chromosomes. Here in Phrynotettix, this spireme condition is more extensive than in any of the Acridadae that I have observed or seen described. Coming from the last spermatogonial telophase as an elongated mass of chromatin, usually club-shaped with the small end of the club attached to the polar elements, it begins to expand in the early thin thread stage (leptotene) with a more or less irregular longitudinal split in the middle. This expansion continues until a loop is formed of a well defined, thick and dense thread. This loop may expand to such an extent that it will form a great circle just inside the nuclear wall. These various stages are shown in figures 13 & 17. As the cells pass into the double thread stage this extended loop begins to contract and soon assumes the condition of a homogeneous mass of chromatin, at first club-shaped as before and then more or less rounded in

Figs 18, 19, 20.
outline. This latter condition is maintained through the rest of the growth period but when the spireme begins to break up into tetrads the accessory again becomes thread like, but this time it is thicker, denser, not looped, but more or less coiled, though a faint longitudinal split may show in one end. This coiled condition is followed by a gradual condensation through the early prophases where it goes through the customary L, U, and J shapes, to become a straight smooth rod as in other forms. Like the other forms also it becomes rough in the metaphase and proceeds to one pole undivided, usually slightly in advance of the other chromosomes, as Miss Pinney has already recorded.

The parallelism between the accessory and the precocious element lies in the following facts: a. Both possess a consistent differentiation from the other chromosome in the growth period by means of a similar property, namely, greater degree of condensation; as shown by deeper staining; b. Early differentiation in the telophase of the last spermatogonia; c. A precocious approach to the poles in the anaphase of the first spermatocyte; d. A similar non-diffusing condition in the telophase of the first spermatocyte; e. A similar persistence for a time in the young spermatid. In most of these stages the difference in their respective conditions and behaviors was one of de-

gree only, not overlooking, of course, the fact that the accessory is a dyad where the precocious element is a tetrad until after the first spermatocyte division.

The significance of this parallelism may be that in this precocious element we have a transition mode of behavior between the ordinary type of chromosome and the idiochromosome type. And by "idiochromosome type" I mean to include the accessory chromosomes and the idiochromosomes, the latter of the nature of those described by Wilson for the Hemiptera. Since, as pointed out by Wilson (11), the accessory may represent a persisting one of a pair of idiochromosomes, the two are seen to be of the same type.

D. The Precocious element in other forms.

With this element as in the case of the polar granules, its presence in Phrynotettix led to a search for it in other forms and, as with the granules, it was found to exist in a number of other species of Acridadae. With the exception of Hadrotettix, however, the element was not so prominent nor so well differentiated in any of the other forms studied, and in some it appeared to become differentiated only in the later stages of the growth period. In a number of the species examined a precocious member of the metaphase group was found that behaved precisely as does the one in Phrynotettix, but the preparations did not show well the details of the spireme stages, so that I do not consider that a failure to observe it proves its absence

there. Theforms in which a condensed loop of the spireme has been definitely made out were species of Hadrotettix, Brachystola, Hippiscus, Amphitornus, Hesperotettix, Stenobothrus, Arphia, Aeoloplus, Phaetoliotes, Pamphagus, and Melonoplus. The identity of this differentiated spireme loop with one of the metaphase chromosomes has not been definitely established in all the forms named but such an identity has been found in Brachystola, Hadrotettix, Arphia, and Melonoplus, and it may consistently be thought to exist in the other species. Davis (2) describes in his paper what he calls a double monosome, his term monosome being applied to the accessory. I have examined some slides of Melonoplus Bivattatus furnished me by Miss Nowlin and I find in it the same precocious spireme loop thread that I find in the other forms and its identity with the precocious tetrad described by Miss Nowlin for this species is well established. Figures 41, 42, 43 show successive stages where the precocious thread becomes transformed into a tetrad. I think that this is undoubtedly the same element that Davis figures as a "less dense" and thread-like part of his monosome in M. Femaratus. The association of the accessory and this precocious element does not seem to be as constant in Phrynotettix and some other forms as Davis figures for Melonoplus Femaratus, but I think that there is no doubt about this thread forming a separate tetrad. His figures 119 to 123 indicate this very strongly. The same criticism can be

offered in the case of Stenobothrus where his figures will more strongly parallel my figures for Phrynotettix.

While making a study of this material a number of other peculiarities have been encountered but, as stated at the beginning of this paper, their history has not yet been determined definitely enough to be described here and they must be left for the future.

IV. Summary of Observations.

1. The polar granules tend to unite, fuse, or coalesce, not only through the growth period at the center of the rosettes but also in the spermatogonial telo- and pro- phases and in the same phases of the connective tissue and follicular cell muclei.

2. The composite granules (chromoplasts) thus formed in the growth period, are composed of the polar granules not only of a variable number of chromosomes but also of a variable individual constituency.

3. A continuous spireme resulting from an end to end union of chromosomes is found not only in the telophase of the last spermatogonial division and continuing through the growth period, but also in the telophase of the other spermatagonial generations and, to all appearances, in the connective tissue and follicular cell nuclei. This process is of course related to that of the formation of the composite granules.

4. Similar granules are found in many of the Acridadae

and in Gryllus. The Chromoplast of Janssens in Batrachoceps appears to be homologous to the composite granules.

5. One of the spireme loops shows an individuality of behavior by its greater degree of condensation and precocious behavior throughout the first spermatocyte stages: growth period, prophases, metaphase, and telophase; and in the young spermatid. A similar element was observed in a number of species of the Acridadae.

6. The Accessory undergoes a more extensive spirematic condition than in most other forms.

V. Summary of Conclusions.

1. Miss Pinney's conclusions as to the permanent polarization of the chromosomes is an expression of the complete but complex organization of the nuclear substance through nearly all stages of its history. This is also indicated by the composite granules and the continuous spireme.

2. The Precocious member of the series of chromosomes may represent a transition mode of behavior between the ordinary type of chromosome and the idiochromosome type.

3. The behavior of this precocious member is an additional argument, if any is needed, for the individuality of the chromosomes.

4. Every time an additional chromosome is found whose individual history and behavior can be determined, an additional

iota is contributed toward the solution of the problem of the relation of individual chromosomes to body characters.

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Explanation of Plates.

(These drawings were made with the aid of a Spencer 2 m m objective and a Zeiss No. 12 compens. ocular. They were outlined with the aid of a camera-lucida.)

Plate I.

Figs. 1 and 2. Connective tissue nuclei, in telophase stage. Composite granules at z and z^1.

Fig. 3. Telophase of primary spermatogonia. Composite granule at z.

Fig. 4. Prophase of an early generation of the secondary spermatogonia. Composite granule at z.

Fig. 5. Telophase of spermatogonia showing union of chromosomes in pairs at the proximal or synaptic end. Accessory at x.

Fig. 6 and 7. Telophase of spermatogonia showing continuaus spireme formation.

Fig. 8 and 9. Telophase of spermatogonia showing granules at both ends of some of the chromosomes. Vesicular accessory at x.

Fig. 10. Later telophase of spermatogonia showing twelve polar granules (reduced number). Accessory at x.

Fig. 11. Telophase of spermatogonia showing some of the granules fused into composite granules (at z z^1). Accessory at x.

Fig. 12. Late telophase of spermatogonia showing early condensation of precocious element (at y). Accessory at x.

Fig. 13 to 17. Early growth stages showing gradual expansion of accessory (x) into a loop. Composite granules at z, z^1, z^{11}, z^{111}.

Fig. 19. Shows accessory (x) contracted again after its expansion. Composite granule at z.

PLATE I

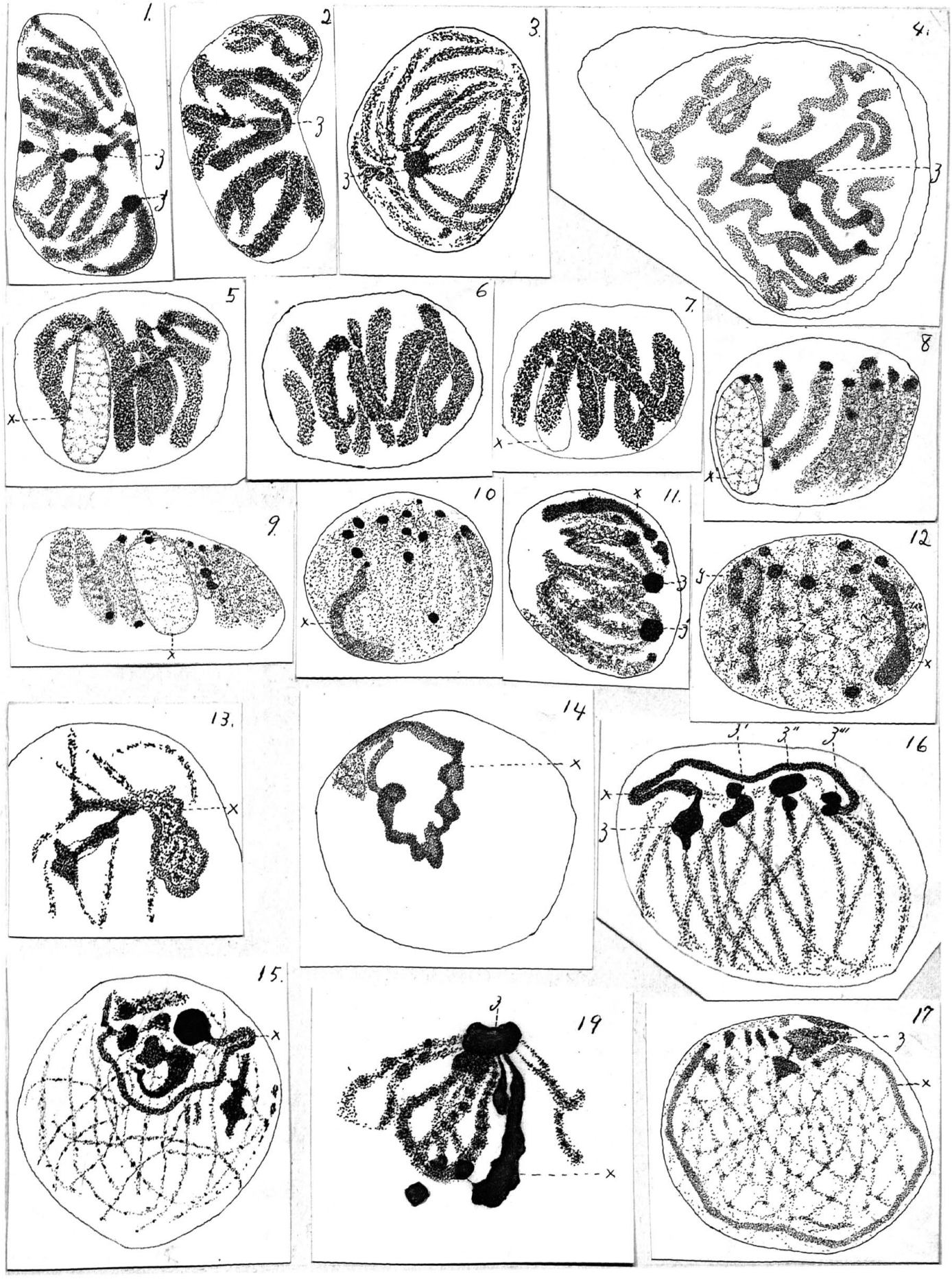

1.
3
3
2
3
3.
3
4.
3
5
x
6
7.
x
8
x
9
x
10
x
11.
x
3
3
12
3
x
13.
x
14
x
16
3'
3"
3'''
x
3
15.
x
19
3
x
17
3
x

Plate II.

Fig. 18. Shows early stage in the contraction of accessory (x) after its expansion. (Figs. 13-17). Composite granule at z.

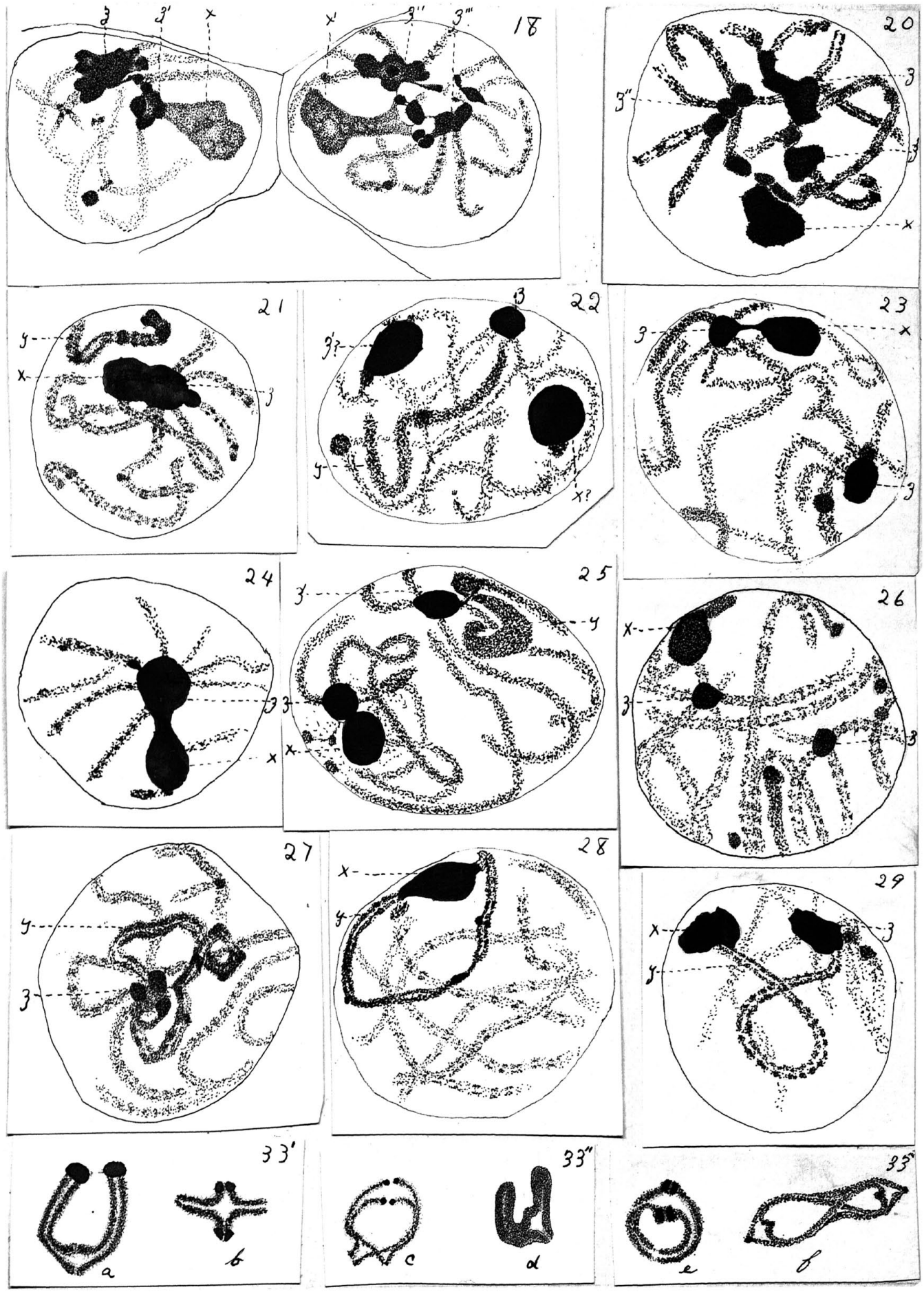
Fig. 20. Polar view of early thick spireme stage (Pachytene stage) showing composite granules (z, z^{1}, z^{11}) in process of formation. Accessory at x.

Figs. 21- 26. Examples of growth period nuclei in resting condition (Pachytene stage) showing composite granules (z) and the accessory (x) in various relationships. Precocious element at y.

Figs. 27-29. Growth stage nuclei showing various relationships between the precocious loop (y), the accessory (x) and the composite granules (z).

Fig. 33. Various tetrad figures showing granules. Precocious tetrad at d. Gramules at both ends at f.

PLATE II


18
3
3'
x
x
3''
3'''
20
3''
3
3'
x
21
y
x
3
22
3
3'?
y
x?
23
3
x
3
24
3
3
x
25
3
y
3
x
26
x
3
3
27
y
3
28
x
y
29
x
3
y
33'
a
b
33''
c
d
33'''
e
f

Figs. 41, 42, and 43, are of Melonoplus. Fig. 41, Growth stage showing accessory (x) and precocious spireme loop (y). Fig. 42, shows tetrads in prophase of first spermatocyte. Precocious tetrad at y. Fig. 43, of metaphase, first spermatocyte, shows precocious division of precocious tetrad (y), accessory at x.

Plate III.

Fig. 30. Growth stage showing relation of precosious spireme loop (y) to composite granule (z).

Fig. 31. End of growth stage showing composite granule (z) breaking up into its component granules.

Fig. 32. Nucleus showing tetrads fully formed from spireme loops and showing polar granules. Precocious tetrad at y.

Fig. 34. Metaphase, first spermatocyte, showing precocious division of precocious tetrad y.

Fig. 35. Telophase of first spermatocyte showing accessory (x) and precocious (y) dyads compact while all others are diffuse.

Fig. 36. Telophase of second spermatocyte showing composite granule (z), accessory (x), and precocious element (?) (y).

Fig. 37. Spermatid showing some persisting granules, the accessory (?) (x), and the precocious element (?) (y).

Fig. 38. Growth stage of Brachystola showing precocious spireme loop (Y), and accessory (x).

Fig. 39. Telophase of spermatogonia in Dissosteria showing a section of continuous spireme.

Fig. 40. Growth period in Gryllus showing accessory (x) and composite granule (?) (z).

PLATE III